Soil properties and microbial activity across a 500 m elevation gradient in a semi-arid environment

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Abstract

If climate change causes the semi-arid shrub-steppe to become hotter and drier it may affect soil C and N cycling and precipitate changes in soil processes and microbial and plant community structure. This study was conducted, using an elevation gradient as an analog of climate change, to analyze climatic influence on soil microbial activity and soil properties. We collected soil from under cryptogamic crust and bunchgrass plants at 25 sites over a 500 m elevation transect in a shrub-steppe ecosystem located in eastern Washington State of the US. The samples were analyzed for several chemical and microbiological attributes including pH, microbial biomass and nitrification potential and the data grouped into five climate sites for statistical analysis. Soil pH decreased over the transect with higher pH values in the grass soil than the crust. In contrast soil electrical conductivity (EC) increased with increasing elevation as did both ammonium and nitrate. Ammonium and EC were greater in the crust soil than the grass soil but nitrate concentration was the same under both plant covers. Both total C and N amounts increased with elevation as did nitrification potential. Due to high sample spatial variability microbial biomass, respiration and N mineralization showed non-significant trends over the 500 m elevation transect. Using these measured gradient relationships the increase in temperature and decrease in precipitation that is expected in this shrub-steppe ecosystem over the next 100 years would eventually cause the pH to increase and the EC to decrease. Plants would become more sparse, nitrification potential would decrease and ammonium would increase. Total C, N and microbial biomass concentrations would begin decreasing and may shift the controlling factors of the ecosystem to abiotic factors. The changes in the cycling of N and to some extent C due to climate change could alter the microbial and plant community structure and function of this ecosystem and cause it to move in the direction of desertification. Published by Elsevier Science Ltd.

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1. Introduction

Recent events in the world's political arena have increased attention on global warming and its effect on the Earth. Traditionally, the effects of global climate change have focused on food production, geographic climate shifts and large effects such as rising sea levels. Recently, attention has focused on the potential changes in terrestrial ecosystems that might result from climate change (Walker and Steffen, 1999). Of particular interest are shifts in the distribution and quantities of soil organic matter (SOM), which may have a relatively short response time ($10–10^2$ years) and might be a sensitive indicator to projected warming trends (Franz, 1990). However, less attention has been given to the effects of climate change on soil processes and function (Lal et al., 1995), even though many terrestrial changes will be a direct result of the changes in soil properties and processes.

Arid and semi-arid ecosystems represent over 25% of the Earth's land area and are increasing in proportion due to desertification (Emanuel et al., 1985; Houghton, 1997). The soils in these ecosystems characteristically contain less SOM and plant biomass than other terrestrial ecosystems, suggesting that even a small climate change may significantly impact changes in soil properties and processes, in particular C and N cycling (West et al., 1994). West et al. (1994) indicated that these lands may be the first terrestrial ecosystems disrupted as a result of climate change because of the fragile nature of the soils. Thus studies of arid and

semi-arid ecosystems may provide enhanced information of the ecological consequences of climate change and suggest the most useful measurements to detect changes in these and other ecosystems.

One major semi-arid ecosystem is the shrub-steppe, the largest grassland-type ecosystem in North America (Rogers and Rickard, 1988). An area in southeast Washington State contains some of the last remaining shrub-steppe that is in near pristine condition (Rogers and Rickard, 1988). Undisturbed plant communities in the shrub-steppe are dominated by big sagebrush (*Artemisia tridentate Nutt*) and perennial grasses (*Pseudoregneria spicata Prush* and *Poa secunda Presl*) growing with a thin cryptogamic (lichens and moss) crust covering much of the interplant areas. Soils are typically loess-overlying basalt and the climate is characterized as semi-arid, temperate, and continental with cold, wet winters and hot dry summers (Rickard, 1988).

We used a 500 m elevational transect up a mountain in the shrub-steppe to simulate a climate change scenario (Smith and Bolton, 2000). The maximum temperature decreases over the transect by 7 °C and the annual precipitation increases by 10 cm thus the higher elevation is cooler and wetter than the lower elevation. This climate regime has been stable for the last 3000–5000 years (Gaylord and Stetler, 1994).

This transect in the semi-arid shrub-steppe is unique in that the parent material, loess, the dominant grass vegetation and soil texture are similar over the 500 m elevation gradient, suggesting that differences in soil chemical and biological properties across the elevation gradient are potentially related to differences in climate. In addition, we constrained as much as possible the factor of topography (slope and aspect) in the sampling scheme. Thus, unless there were major influences on soil properties from unknown biogeochemical constraints we should be able to hypothesize the direction of change of soil attributes due to future shifts in climate.

Our objective was to measure soil abiotic and biotic parameters in several isothermal zones across a significant elevational transect and relate these parameters to differences in climate (e.g. hotter/drier and cooler/wetter). The hypothesis was that zones with different climate regimes would have different soil attributes and differ in the cycling of C and N. We also wanted to determine if the grouping of spatially explicit samples across a distance would provide a more robust analysis of differences between zones. In addition, we were interested in these properties and processes relative to plants and cryptogamic crust over the landscape.

2. Materials and methods

2.1. Field site and soil collection

The study site is located on the Fitzner–Eberhardt Arid Land Ecology (ALE) Reserve contained within the US

Department of Energy's Hanford Site in southeastern Washington State. The ALE Reserve is the only remaining sizable (31,200 ha) area of Washington shrub-steppe that has not been directly disturbed by humans since the early 1940s. The ALE Reserve has a semi-arid climate with two-thirds of the 10–28 cm of precipitation occurring during the winter (Rickard, 1988). The dominant plant species include big sagebrush (*Artemisia tridentata*), bluebunch wheatgrass (*P. spicata*), and Sandburg bluegrass (*P. secunda*) with a cryptogamic lichen and moss crust covering much of the undisturbed interplant soil area (Link et al., 2000).

The vegetation at the sampling sites is dominated by *P. spicata* with the cryptogamic crust occupying interplant spaces (Bolton et al., 1993). On an aerial basis the percentage of the crust cover decreases with increasing elevation while the plant cover increases. The silt loam soil at each site was formed from the same loess parent material (basalt) deposited over this area in the last 3000–5000 years. The mean clay content in the top 5 cm is 4.9% and the mean silt content is 52.2% with a slight, but not significant decrease in silt concentration with elevation from 53 to 49%. The dominant mineral of the clay fraction is montmorillonite.

We sampled at locations arrayed in an elevation transect up the slope of Rattlesnake mountain (1093 m) located on the ALE reserve. Twenty-five sites were identified for sampling starting at an elevation of 228 m and continuing every 25 m to a maximum elevation of 844 m. Average precipitation increases from 180 mm at the lowest elevation to 270 mm at the 844 m elevation site (Fig. 1). Conversely, the mean annual maximum temperature decreases from 30 °C at the 228 m elevation site to 24 °C at the top of
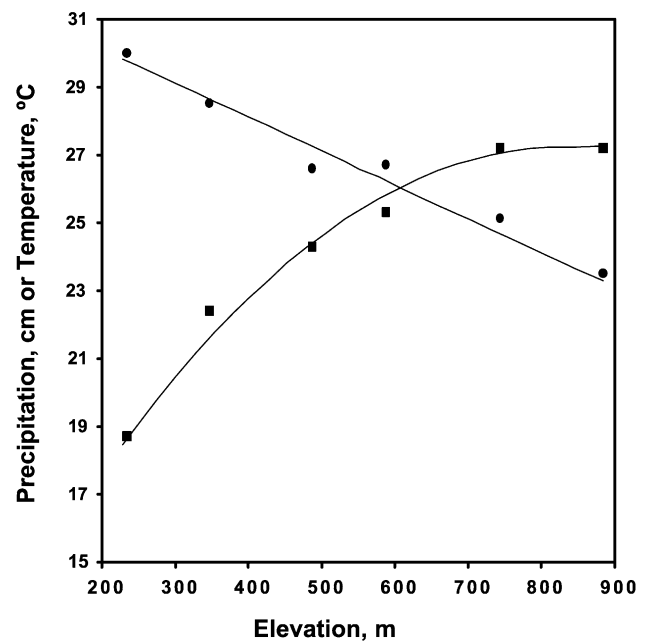

Fig. 1. Mean maximum temperature (●) and annual precipitation (■) for the shrub-steppe elevation gradient in eastern Washington, US.

the transect. However, considerable microclimatic variability exists along the elevation gradient (Hinds and Thorpe, 1969).

We collected four soil samples at each site from the 0 to 5 cm depth, under the crust and *P. spicata* plants using a hand spade. Each sample was placed in a plastic container in the field and kept cool until processed in the laboratory. Initial processing included sieving the samples through a 2 mm screen and determining the gravimetric moisture content on subsamples after drying at 105 °C.

Exploratory data analysis summary statistics, from moving windows analysis and bivariate scatter plots, showed spatial continuities in the data with elevation. Using this spatial continuity we grouped the 25 sites into five temperature and precipitation zones with five nearest neighbor sites in each zone. The midpoint site represented the actual elevation that is reported for the data (i.e. midpoint sites were 301, 426, 552, 684, and 810 m). Each of the five zones incorporated all of the data collected in a 120 m elevation increment (20 per site per soil cover type). Each zone over the transect differed from its nearest neighbor by ± 1.5 °C and ± 1.8 cm precipitation.

2.2. Chemical and biological analyses

Soil samples were analyzed for pH and electrical conductivity (EC) using a 1:1 soil-deionized water paste. A 10 g subsample of soil was extracted with deionized water for soluble C analysis with an infrared CO_2 analyzer (Smith et al., 1994). A separate 10 g subsample of fresh soil was extracted with 2 M KCl for determination of inorganic N (NH_4-N and NO_3-N) using an auto-flow colorimetric procedure. Total C and N was determined by dry combustion in a continuous flow system with the combustion chamber at 1000 °C. The elemental analyzer has a precision of 13 ppm C (0.0013%) and 6 ppm N (0.0006%) for sample sizes up to 1 g.

Microbial biomass carbon was determined using the substrate induced respiration method (SIR) after Anderson and Domsch (1978). Duplicate 10 g samples were weighed into 40 ml glass vials, brought to field capacity (18% w/w, -33 kPa), covered and kept in the dark for 7 days at 22 ± 0.5 °C. At the end of the preincubation each sample received 0.5 ml of 150 mmol l^{-1} glucose solution. Control samples received 0.5 ml of water. All tubes were flushed with hydrated air and covered. After 2 h the vials were capped with a septum and headspace CO_2 was measured 1 h later from each vial by injecting 0.2 ml into a gas chromatograph equipped with a porpack Q column and thermal conductivity detector. Microbial biomass C was calculated using the equation published by Anderson and Domsch (1978).

Dehydrogenase activity was estimated using the TTC (triphenyltetrazolium chloride) method without the addition of glucose (Bolton et al., 1993). Triplicate 1.5 g soil samples were incubated for 24 h with TTC and the reduction product triphenylformazan (TPF) was measured by colorimetry. The results were compared to standard TPF solutions and reported as μg-TPF g^{-1}-soil 24 h^{-1}.

The nitrification potential assay consisted of incubating duplicate soil samples (10 g), amended with 100 μg-N g^{-1} $(NH_4)_2SO_4$, for 1 week in the dark at 22 °C. After the incubation the samples were extracted and analyzed for NO_3^--N, the potential nitrification is the net increase of NO_3^--N.

Mineralizable C and N were determined over an 18 day incubation period at 22 °C. Ten-gram soil samples were placed in 40-ml glass vials and soil water was adjusted to 18% w/w (-33 kPa) before being capped with a septum. Headspace CO_2 concentration was analyzed by gas chromatography every 1–3 days during the incubation. The incubation vials were flushed with CO_2 free air after sampling to prevent CO_2 concentrations from becoming too high during the next incubation period. After the last CO_2 measurement the soil in each vial was extracted with 2 M KCl for the analysis of NH_4^+-N and NO_3^--N. The net nitrogen mineralized during the incubation equaled the N mineralization potential.

Statistical analysis for the effects of elevation and vegetation cover type was conducted using a two-way ANOVA model. Post hoc tests for each variable were made using Bonferroni pairwise comparisions (SPSS, 1998). Hydrogen ion concentration was used for the statistical analysis of pH.

3. Results

3.1. Elevation transect

This elevation gradient in the shrub-steppe provides a unique opportunity to evaluate the effects of in situ temperature and precipitation on soil nutrient pools and microbial activity. In the five climate zones (25 sites total) established over the 500 m transect actual sampling locations were on < 10% slopes and < 40° in aspect from North. Even with these constraints the spatially explicit samples (non-composite) and resulting data showed significant amounts of variability in some soil abiotic and biotic parameters. The variability within sites was similar to between sites within zones and ranged from about 6% coefficient of variation (CV) for soil pH to more than 50% for microbial respiration. This makes statistical differences difficult to prove and thus trends in the data were also explored.

3.2. Chemical pools

Soil pH decreased with increasing elevation over both soil types (Fig. 2(a)). In addition, the crust soil had lower pH values than the grass soil over the transect with mean values 5.9 and 6.2, respectively (Fig. 2(b)). The effects of elevation
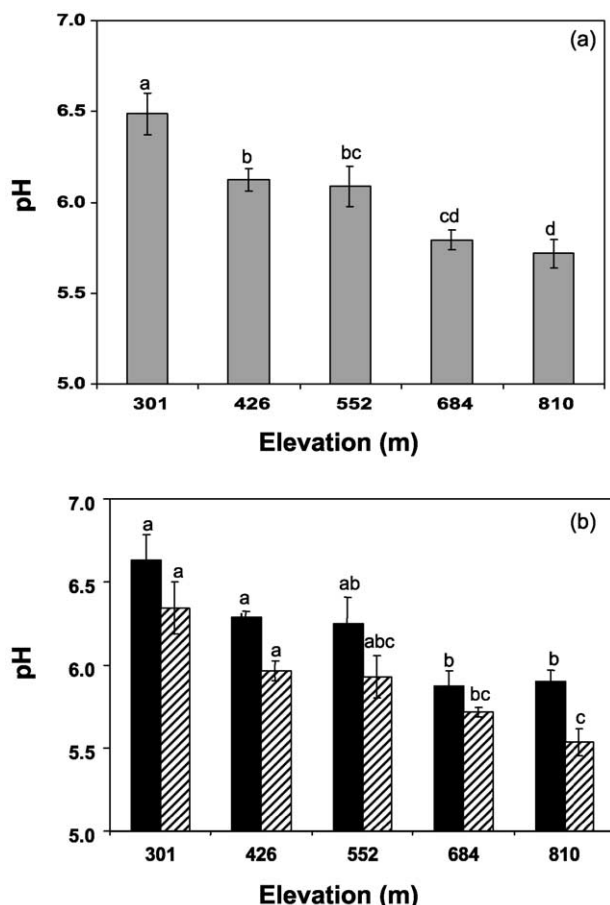
Fig. 2. Changes in soil pH along a 500 m elevation gradient, (a) overall effects (b) cover type effects. Letters in (b) indicate significant differences within cover type over the elevation transect. Values are means ± SE.
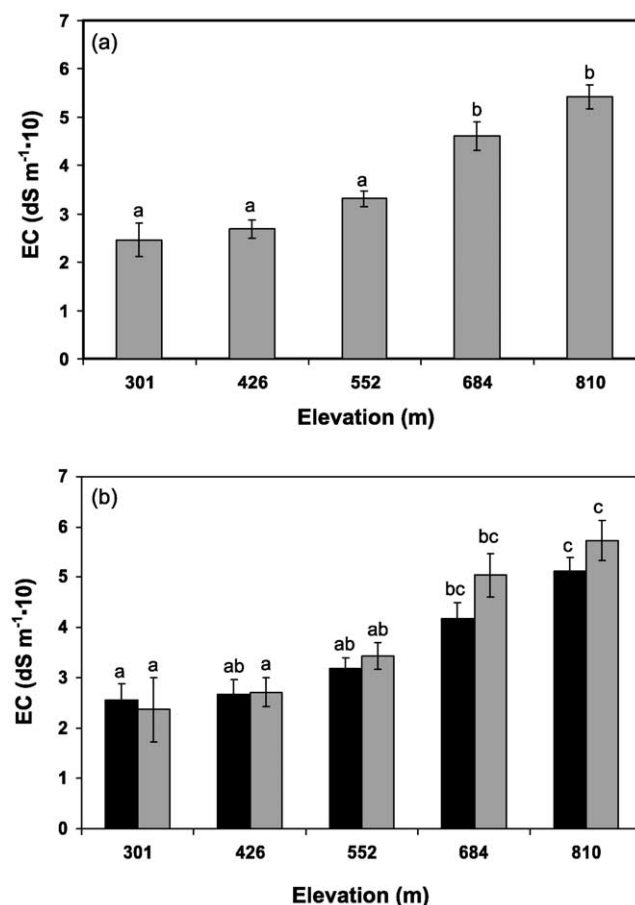

Fig. 3. Changes in soil EC along a 500 m elevation gradient, (a) overall effects (b) cover type effects. Letters in (b) indicate significant differences within cover type over the elevation transect. Values are means ± SE.

and cover type were both highly significant ($P = 0.001$) with no with statistical interaction. There were similar trends within the grass or crust soil with the lower sites being more alike and greater than the upper sites (Fig. 2(b)).

For the overall means soil EC increased with elevation with the top two sites significantly greater than the lower sites (Fig. 3(a)). There was no significant difference between grass and crust soil ($P = 0.18$). However, there was a greater EC increase in the crust soil with increased elevation as compared to the grass soil (Fig. 3(b)).

Nitrate from soil under grass increased from 14 µg $NO_3 - N\ g^{-1}$-soil at the lowest site to over 26 µg NO_3-$N\ g^{-1}$-soil at the upper site, similar concentrations were found in the crust soil (Table 1). In contrast NH_4^+N was low in the grass soil but increased with elevation over the transect in the crust soil from 2 to 7 µg NH_4^+-$N\ g^{-1}$-soil. There was a significant increase in NH_4^+-N and NO_3^--N with increasing elevation ($P < 0.05$ and 0.01, respectively). However, there was only a significant difference in cover type for NH_4^+-N concentration (Table 1). Soluble C was similar in concentration over

the transect but there was significantly greater amounts in the grass soil than the crust soil (Table 1).

Fig. 4 shows the soil total organic carbon and soil total organic N as a function of elevation for soil sampled under

Table 1

Mean values and statistical differences of several soil parameters measured over the 500 m elevation transect

Parameter	Cover type (m)				ρ^{a}	
	Grass		Crust			
	301	810	301	810		
Soluble C (µg-C g^{-1}-soil)	35.5	40.8	24.4	26.5	ns	*
Dehydrogenase (µg-TPF[b] g^{-1}-soil)	43.8	47.6	45.4	40.9	ns	ns
NH_4-N (µg-N g^{-1}-soil)	0.9	1.4	2.0	7.0	**	*
NO_3-N (µg-N g^{-1}-soil)	14.4	26.8	10.9	28.4	*	ns

[a] The first column signifies differences in the parameter due to elevation and the second column signifies differences in the parameter due to cover type. ns, non-significant; *$P < 0.01$, **$P < 0.05$.

[b] µg Triphenylformazan g^{-1}-soil 24 h^{-1}.

grass and crust cover types. Soil C concentrations significantly increased ($P < 0.001$) with elevation with greater increases associated with grass than crust soils (Fig. 4(a)). In addition, soil C concentrations were significantly greater ($P < 0.001$) in soil under grass cover (20 g kg^{-1}) than soil under crust cover (14 g kg^{-1}). In general, the top two sites contained significantly greater ($P < 0.05$) C than the lower three sites (Fig. 4(a)). Soil N concentrations showed less of an increase with elevation than did C (Fig. 4(b)). However, overall differences in elevation for N concentrations were significant ($P < 0.01$). In addition, the soil N was significantly greater ($P < 0.05$) in the grass soil (3.7 g kg^{-1}) compared to the crust soil (3.0 g kg^{-1}). The C/N ratio for both soils is low, overall the grass soil had a significantly greater ratio 5.4 than the crust soil 4.5 ($P < 0.05$).

3.3. Soil microbial biomass and biological activity

There was no significant difference in microbial biomass with elevation (Fig. 5(a)) however, there was significantly ($P < 0.05$) more microbial biomass in the crust soil (750 µg C g^{-1}-soil) than the grass soil (674 µg C g^{-1}-soil).

For individual random samples respiration was highly variable and like soil microbial biomass there was no significant differences among elevations ($P < 0.70$) (Fig. 5(b)). However, similar to biomass C there was significantly ($P < 0.01$) more respiration from the crust soil (380 µg C g^{-1}-soil) than the grass soil (300 µg C g^{-1}-soil). These activity measurements were mixed in comparison to soil dehydrogenase enzyme activity, which showed no significant differences with elevation or cover type (Table 1).

Nitrification potential increased slightly in grass and crust soil with increasing elevation, however, due to high sample variability the increase was not statistically significant (Fig. 6(a)). Crust soil exhibited significantly ($P < 0.001$) lower nitrification potential than the grass soil (15 vs 28 µg N g^{-1}-soil d^{-1}) (Fig. 6(a)). Overall there was no significant trends of N mineralization with elevation, although, in contrast to nitrification potential there was significantly ($P < 0.002$) more mineralization in the crust soil than in the grass soil (50 vs 44 µg N g^{-1}-soil d^{-1}) (Fig. 6(b)).
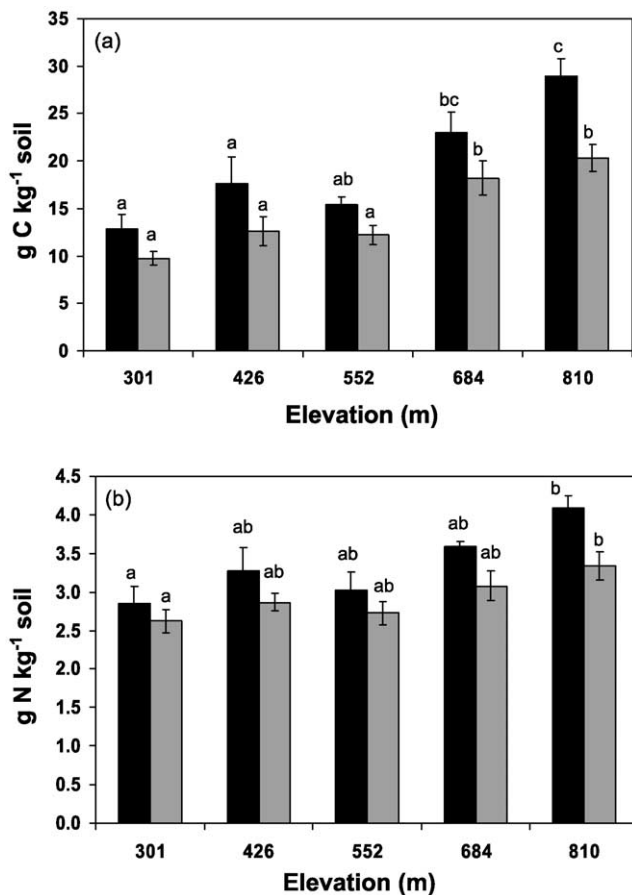

Fig. 4. Total soil C and N concentrations over a 500 m elevation transect in a semi-arid shrub-steppe. Letters indicate significant differences within cover type over the elevation transect. Values are means ± SE.
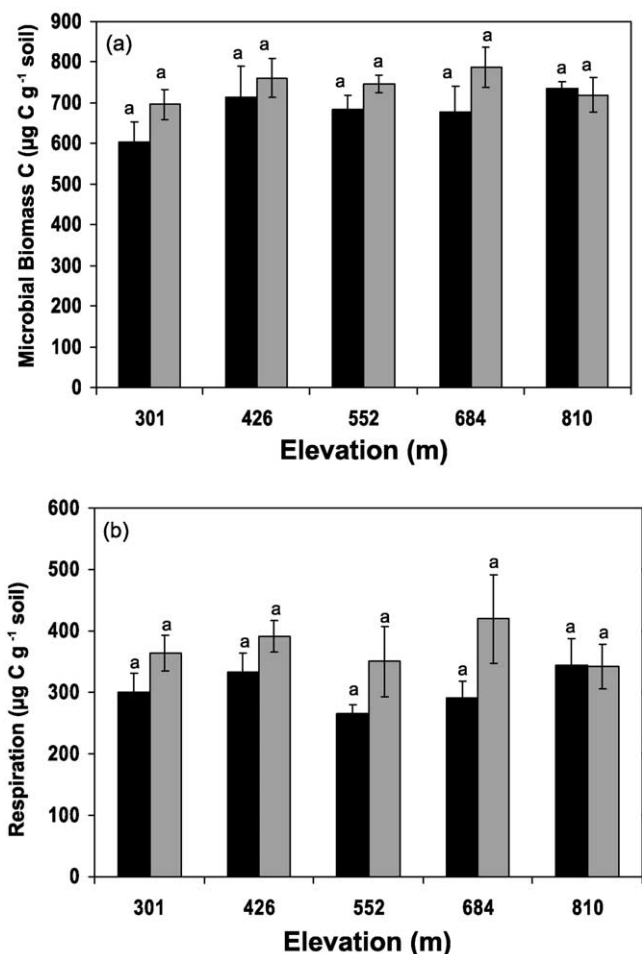

Fig. 5. Microbial biomass C and 18 day cumulative C respiration for crust and grass soils at five elevation sites along a transect in a semi-arid shrub-steppe. Letters indicate significant differences within cover type over the elevation transect. Values are means ± SE.
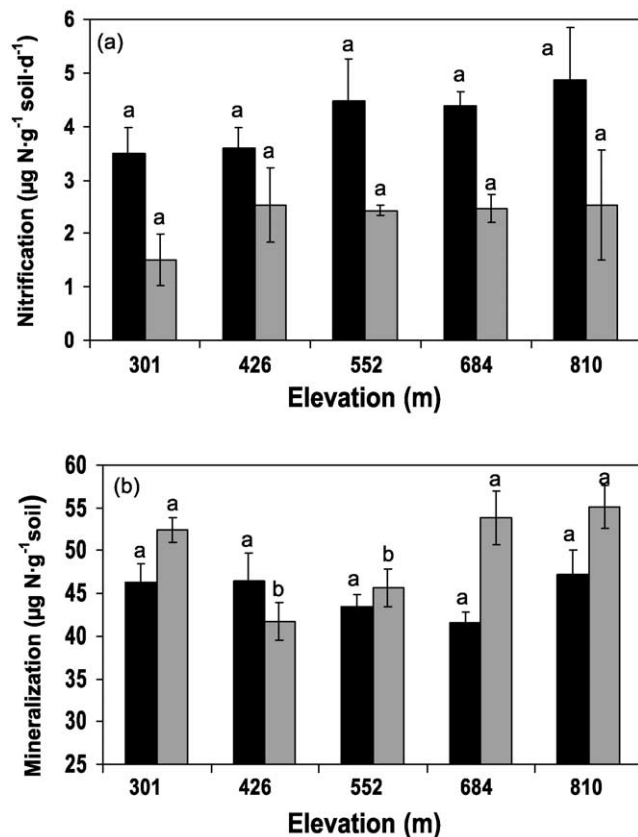
Fig. 6. Nitrification potential and 18 day net N mineralization for crust and grass soil over the 500 m transect in a semi-arid shrub-steppe. Letters are significant differences within cover type over the elevation transect. Values are means ± SE.

4. Discussion

4.1. Soil chemical attributes

Soil pH is a function of parent material, time of weathering, vegetation and climate. Since time of weathering and vegetation type are similar for all locations along the ALE transect the trends of decreasing soil pH could be due to increased leaching of basic cations in the higher elevations from greater precipitation and from increased nitrification. An acidic rhizosphere effect from both plants and lichens could also cause a decrease in pH with elevation. The decrease in pH was also reported for an oak woodland-confier forest elevational transect in the western US (Dahlgren et al., 1997) and higher elevation pine forests in the eastern US (Stanko-Golden et al., 1992).

The increase in EC with elevation (Fig. 2(a), (c) and (d)) would seem to contradict the hypothesis that the leaching of bases is causing the lower soil pH values with increasing elevation. However, in both the grass and crust soil there was a significant amount of nitrate in the higher elevations (Table 1) which could contribute to the increase in EC over

the 500 m elevation transect (Smith and Doran, 1996) as could greater H^+ ion concentrations from the lower pH. However, most of the contribution to elevated EC probably comes from increased cation exchange capacity (CEC) with elevation due to increased organic matter. Wildung and Garland (1988) reported soil CEC increasing from 11 to 40 $cmol\,kg^{-1}$ with elevation in this ecosystem, more than enough capacity to account for the increase in EC over this transect.

In both soil cover types there was a significant negative Pearson correlation coefficient between pH and EC, $r = -0.53$ ($P < 0.001$) and $r = -0.58$ ($P < 0.001$) for the grass and crust soil, respectively. Whereas, there was a significant positive correlation between EC and nitrate of $r = 0.66$ ($P < 0.001$) for the grass soil and $r = 0.81$ ($P < 0.001$) for the crust soil. Both of these relationships have also been documented in agricultural soils (Smith and Doran, 1996).

4.2. Soil total C and N

The total soil C in this ecosystem increased with elevation in both cover types probably due to the greater precipitation at the higher elevations and associated greater amounts of plant biomass and a thicker soil crust. Lower average annual temperature, retarding decomposition might also result in a greater amount of C sequestration in soil at the higher elevations. Although the range of differences in soil N concentration is small (2.6–4.1 $g\,kg^{-1}$) N increased with elevation and soil type which may be a function of longer residence time of the N in the litter and decreasing soil N losses. In addition, the upper sites may be less susceptible to gaseous loss of N from periodic precipitation onto dry soil (Mummey et al., 1994, 1997). The concentrations of soil C and N were significantly correlated with EC ($r = 0.61$, $P < 0.001$ and $r = 0.46$, $P < 0.001$, respectively), nitrification potential ($r = 0.54$, $P < 0.001$ and $r = 0.53$, $P < 0.001$, respectively) and with each other ($r = 0.86$, $P < 0.001$) suggesting the EC may be a good indicator of organic matter and C and N cycling at these sites.

The relatively narrow range of C and N concentrations provides strikingly low C/N ratios which we first observed in 1989 in soil associated with plants or crust (Bolton et al., 1990; Halvorson et al., 1997). In truly interplant spaces 'bare soil' C/N ratios are on the order of 13–16 (Link et al., 2002). However, for the plant associated soil in this study the C/N ratio increases from 4 to 7 in the grass soil and 4–6 for the crust soil as elevation increases over the 500 m transect. This can be attributed to a slower decomposition rate in the higher elevation sites. With slower decomposition it is possible that the C sequestration mechanisms and C pools would be different from the bottom to the top slope. The conservation of nitrogen is important in this ecosystem and the buildup of N could be due to increases in humic acids of low C/N ratio (Wildung and Garland, 1988) and the enhanced

storage of N in particulate organic matter fractions with low C/N ratios (Rodionov et al., 2000). Thus, change in climate to warmer and drier conditions could disrupt the decomposition cycle and cause both C and N to be lost from the upper elevations (Link et al., 2002).

4.3. Microbial biomass and activity

There was no significant difference in microbial biomass with elevation or dehyrogenase activity for both elevation and cover type (Table 1). This is consistent with correlations of biomass and dehydrogenase for this ecosystem (Bolton et al., 1993). However, it is inconsistent with the fact that microbial biomass should positively correlate with increasing soil C (Smith and Paul, 1990). Although, the microbial biomass ranged from 2 to 6% of the total C in the grass soil and 3–8% in the crust soil, somewhat higher than agricultural soils (Smith and Paul, 1990). Bolton et al. (1997) found the crust soil to have lower microbial biomass than the grass soil using the fumigation and PFLA methods. However, they showed a larger number of colony forming units (CFU g^{-1}-soil) for the crust soil. The PFLA method (Bolton et al., 1997) showed greater biomass with more precipitation as was seen by Steinberger et al. (1999) in a desert climatic transect.

The metabolic quotient, defined as basal respiration per unit of microbial biomass C, has been used as a measure of soil ecosystem efficiency (Anderson and Domsch, 1990). Since microbial biomass and respiration were similar over the transect we calculated average metabolic quotients with the grass soil being 1.2 (10^{-3}) similar to 1.3 (10^{-3}) μg CO_2-C μg^{-1} biomass-C h^{-1} for the crust soil. These values are similar to the values found by Smith et al. (1994) in an earlier study of the lower elevation site and are two times greater than those of other natural forest and grassland ecosystems (Smith, 1993). Higher $q CO_2$ values indicate lower substrate quality (Smith, 1993) and a decrease in the efficiency of organism functioning (Anderson and Domsch, 1990). Thus to maintain the microbial community at steady state more recalcitrant pools of C must be used and more CO_2 per unit biomass is released.

The overall soil nitrification potential showed an increasing trend with elevation possibly due to low levels of NH_4-N at the lower elevations limiting the population of nitrifiers. This trend was also consistent with the soil NO_3-N concentration increasing with elevation. The crust soil with a lower nitrification rate than the grass soil had increased levels of NH_4^+-N which also suggests population or activity limitations. However, both of these observations, for elevation and cover type, can be explained by lower soil C/N ratios at the lower sites and in the crust. Lower soil C/N ratios have been shown to be associated with lower nitrification rates. These nitrification rates for both cover types are high for

semi-arid soils (Skujins et al., 1978) and are on the order of magnitude of gross nitrification reported in undisturbed coniferous forests (Stark and Hart, 1997).

The build up of NH_4^+ in the crust soil is consistent with the crust having a greater mineralization rate than the grass soil. The lower net mineralization in the grass soil is likely a function of greater immobilization by microbial biomass and related to significantly more total C and N and soluble C in these soils. The lack of differences in mineralization due to climate was also reported by Jonasson et al. (1993) for two characteristic tundra soils. Morecroft et al. (1992) also found that mineralization did not decrease with elevation in the Scottish Highlands. In contrast, Marrs et al. (1988) found that in a Costa Rican rain forest nitrification and mineralization decreased with elevation under in situ conditions but were not different under laboratory conditions. This was also observed by Kitayama et al. (1998) across altitudes on ultrabasic parent material in Borneo.

Another efficiency function that has been used is qN or the nitrogen mineralized per unit of biomass-C during an incubation (Smith, 1993; Smith et al., 1994). For both the crust and grass soil the average value of qN was 68 (10^{-3}) μg N μg^{-1} biomass-C, similar to previous work at this site where qN was calculated to be 61 (10^{-3}) μg N μg^{-1} biomass-C (Smith et al., 1994). These qN values are about 50% of the qN values for agricultural, forest and grassland soils and indicates N cycling in the shrub-steppe is more efficient (resistant to loss) due to the low inputs of N on a yearly basis (Smith et al., 1994).

Although the microbial communities were possibly different between the grass and crust soil the metabolic C and N efficiencies were similar. We hypothesize that in the present climate plants and crust are controlling the mineralization processes, overriding the climate effect. This is in contrast to Amundson et al. (1989) who concluded that climate was controlling microbial activity and CO_2 production in desert soils. However, these differences maybe a function of laboratory assays verses in situ measurements. Our data indicate the factors controlling microbial activity may be most optimal in the mid-slope positions due to moderate conditions of temperature and moisture, downslope moisture is limiting and upslope temperature is limiting microbial activity.

4.4. N cycling

In the event of climate change, in this area, we should be able to predict the N cycling effects on this shrub-steppe ecosystem although the analysis is complicated by differences in N cycling between the grass and crust soil. In the crust soil there is slower nitrification which may reduce N_2O production and corresponding losses. However, there is a more rapid cycling of N, thus a higher turnover may

actually offset the reduced N_2O production or even increase N_2O production. Mummey et al. (1994, 1997) showed nitrification to be the most important source of N_2O in the shrub-steppe especially after rainfall events on dry soil. These differences in N cycling between the grass and crust soil will be important as the climate shifts to warmer and drier since the proportion of grass soil to crust soil will decrease and precipitation patterns may change.

5. Conclusions

In the next 50–100 years the mean temperature in this shrub-steppe area is projected to increase by 1.6–2 °C (USEPA, 2000) corresponding to a 3 cm decrease in precipitation, similar to differences in our five climate zones. In the context of this study this may cause the upper sites to become more like the mid-elevation sites and the mid-elevation sites to become more like the lower sites over time. Based on our observations, we expect pH at the top and mid sites would begin to increase and the EC to decrease. Plants at the top and mid sites would become farther apart and cryptogamic crust would spread to the inter spaces which would decrease the nitrification potential and increase NH_4^+ in the system. Total soil C and N and the microbial biomass at these locations would decrease over time as primary productivity was inhibited by lower available precipitation and increased evapotranspiration. Mineralization rates at the top and mid elevations would increase but the plant uptake of N would decrease and the increase in NH_4^+ would shift the soil microbial composition. Though we currently predict that more N_2O would be produced from the grass associated soil (i.e. more from the upper elevations) microbial mediated gas flux is also increased by higher temperatures and drier soil. Thus we hypothesize that a change in climate, to warmer and drier, could potentially increase greenhouse gas flux (CO_2 and N_2O) from this particular shrub-steppe ecosystem.

Factors controlling ecosystem function in the shrub-steppe may shift from soil and plant factors to abiotic factors during ecosystem readjustment. The changes in the cycling of N and to some extent C due to climate change will alter the microbial and plant community structure and function of this ecosystem and potentially cause it to move in the direction of desertification.

Acknowledgments

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